



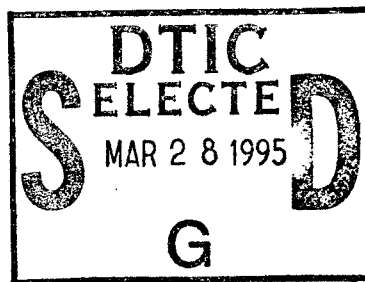
**US Army Corps
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Zebra Mussel Research Program

**Comparative Study of the Desiccation
Resistance of Zebra Mussels (*Dreissena
polymorpha*) and Quagga Mussels
(*Dreissena bugensis*)**

by *Thomas A. Ussery, Robert F. McMahon,*
Center for Biological Macrofouling Research



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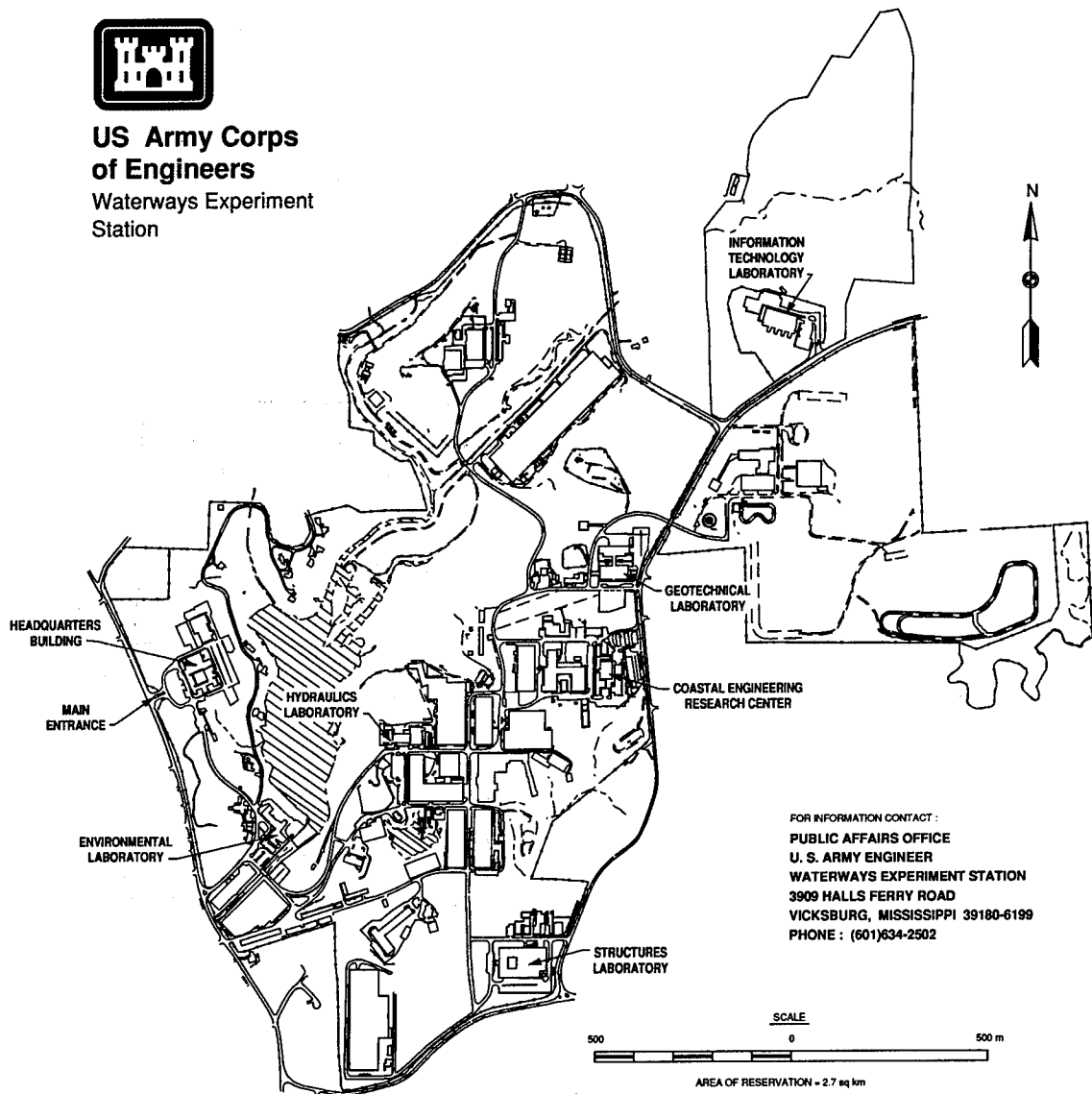
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Preface

The Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990 specified that the Assistant Secretary of the Army, Civil Works, will develop a program of research and technology development for the environmentally sound control of zebra mussels (*Dreissena polymorpha*). As a result, the U.S. Army Engineer Waterways Experiment Station (WES) initiated a program to develop control strategies for this species.

This report was prepared by Mr. Thomas A. Ussery and Dr. Robert F. McMahon, Center for Biological Macrofouling Research, University of Texas at Arlington, Arlington, TX. Dr. Milton A. Matthews and Messrs. Michael Clarke, Michael R. Hernandez, Terry L. Cleland, and Craig A. Burnside of the Center for Biological Macrofouling Research provided editorial assistance with the preparation of the manuscript. Research for this report was funded under Contract DACW39-92-K-0004 with WES. Drs. Andrew C. Miller and Barry S. Payne, Environmental Laboratory, (EL), WES, managed the contract for WES. Dr. Edwin A. Theriot, EL, was Program Manager of the Zebra Mussel Research Program.

During the conduct of this study, Dr. Theriot was Chief, Aquatic Ecology Branch; Dr. Conrad J. Kirby was Chief, Ecological Research Division; and Dr. John W. Keeley was Director, EL, WES.

Dr. Robert W. Whalin was Director of WES at time of publication of this report. COL Bruce K. Howard, EN, was Commander.

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1 Introduction

The zebra mussel, *Dreissena polymorpha*, was introduced to North America in 1986. It originally became established near the Lake St. Clair-Detroit River region. It is believed that mussel larvae were released into the Great Lakes with the ballast water discharge or as adults escaping anchor chains of ships arriving from Europe (Hebert, Muncaster, and Mackie 1989; Mackie et al. 1989; McMahon, Ussery, and Clarke 1993). Since its original introduction, the mussel has spread throughout Lakes Erie, Ontario, Michigan, Oneida, the Finger Lakes, the Erie-Barge Canal, and the St. Lawrence, Hudson, Oswego, Illinois, Mississippi, lower Ohio, lower Tennessee, lower Arkansas, and lower Cumberland Rivers (Zebra Mussel Information Clearinghouse 1993). Zebra mussels are now spreading rapidly throughout North American inland waterways via dispersal of adults attached to commercial barge hulls and downstream transport of their planktonic veliger larvae (McMahon 1992). Reproductive zebra mussel populations are now reported to extend downstream in the lower Mississippi River as far as New Orleans (Zebra Mussel Information Clearinghouse 1993).

Also apparently introduced to the Great Lakes concurrently with *D. polymorpha* was a second species of *Dreissena* originally called the "quagga mussel" (May and Marsden 1992). This second North American dreissenid species was recently identified as the southeastern European species, *Dreissena bugensis* (University of Wisconsin Sea Grant Institute 1993). Specimens of *D. bugensis* have more laterally compressed shell valves than those of *D. polymorpha* and lack the latter species' distinctively flattened ventral shell margins. *Dreissena bugensis* is now found throughout Lakes Erie and Ontario, the St. Lawrence River, and the western portion of the Erie Barge Canal in upstate New York (Dermott 1993), but, unlike *D. polymorpha*, has yet to invade Mississippi drainages (Zebra Mussel Information Clearinghouse 1993). *Dreissena bugensis* is sympatrically distributed with *D. polymorpha* over its present North American range, with the proportion of the two species in dreissenid populations varying greatly on both micro- and macrogeographic scales (Dermott 1993).

Adults of both *D. polymorpha* and *D. bugensis* attach to natural hard substrata such as rocks, wood, and macrophytic plants and to man-made structures constructed of concrete, metal piping, steel, nylon, fiberglass, and wood. Attachment is by a holdfast of proteinaceous byssal threads produced from a

gland just posterior to the foot (Mackie et al. 1989; McMahon 1990). In both species, individuals byssally attach to the shells of other mussels, forming encrusting mats many shells thick (10-30 cm) (McMahon 1990). When such thick encrustations of mussels form on man-made structures or within raw water systems, they negatively impact their operation and efficiency. Because of its capacity for macrofouling, *D. polymorpha* (zebra mussel) has already had major detrimental impacts on recreational boating and commercial shipping as well as on raw water-using industries, potable water treatment plants, and electric power stations in North America (Roberts 1990; Claudi and Mackie 1993).

Presently, the main control technologies for zebra mussel macrofouling center on molluscicides such as chlorine, bromine, ozone, aromatic hydrocarbon compounds, and quaternary ammonium compounds (Electric Power Research Institute 1992). However, federal and state regulations for use of molluscicides in controlling macrofouling by dreissenids and other freshwater macrofouling bivalves (i.e., *Corbicula fluminea*, the Asian clam) are likely to become increasingly restrictive. With the specter of nearly every raw water-using facility on the major waterways of the Mississippi Drainage applying molluscicides to control zebra mussel fouling, and presently increasing mussel infestations of raw water facilities on the Great Lakes, molluscicide usage will be highly regulated in order to prevent water quality degradation and maintain drinking water standards (McMahon, Ussery, and Clarke 1993). Therefore, in order to maintain the quality of North American waterways, an increasingly greater priority is likely to be placed on the development of reliable, cost-effective, environmentally acceptable, nonchemical zebra mussel macrofouling control technologies.

Among nonchemical dreissenid mitigation strategies, dewatering of infested structures to expose mussels to lethal levels of desiccation appears to be a readily applied, efficacious, and environmentally neutral technology worthy of further attention (Claudi and Mackie 1993; Electric Power Research Institute 1993; McMahon, Ussery, and Clarke 1993). Dewatering could be a particularly efficacious means of mussel control in raw water systems such as navigation locks and water intake structures that are designed to be periodically dewatered for maintenance. McMahon, Ussery, and Clarke (1993) have shown that zebra mussels are much less tolerant of emersion than are the majority of native North American bivalves. Mathematical models predicting the duration of emersion required for mitigation of *D. polymorpha* infestations relative to exposure air temperature and relative humidity have been developed (McMahon, Ussery, and Clarke 1993). In contrast, there is no available information on the desiccation tolerance of *D. bugensis*. In raw water systems drawing from the Great Lakes, *D. bugensis* and *D. polymorpha* can form mixed macrofouling populations (Dermott 1993). Thus, if the levels of desiccation lethal to *D. polymorpha* are also lethal to *D. bugensis*, similar durations of dewatering and emersion could be utilized to mitigate fouling by pure populations of either species or mixed populations of both species.

Dreissena bugensis has been reported to be a deeper water species than *D. polymorpha* (Dermott 1993). Restriction to deeper water suggests that *D. bugensis* may be less tolerant of emersion than *D. polymorpha*, whose populations extend nearly to the surface (Mackie et al., 1989) where they can be emersed by natural water level variation. This report presents results of a study comparing the desiccation tolerance of *D. bugensis* and *D. polymorpha*, allowing analysis of the potential for dewatering to be an effective, nonchemical mitigation technology for both species. The results are also utilized to relate desiccation tolerance to differences in the depth distributions of the two species.

2 Materials and Methods

Specimens of *D. polymorpha* were collected from the intake of a power station drawing water from Lake Erie near Cleveland, OH. Specimens of *D. bugensis* were taken from the western basin of Lake Erie near the City of Monroe, MI. They were shipped overnight emersed on moist paper toweling in insulated, cooled containers to the University of Texas at Arlington. On arrival, they were maintained in 284 l of continually aerated, dechlorinated, City of Arlington tap water in a refrigerated "Living Stream" holding tank at a constant water temperature of $5^{\circ}\text{C} \pm 0.5^{\circ}\text{C}$ without feeding for no more than 30 days before utilization in experiments. Specimens of *D. polymorpha* held under these conditions show no significant reduction in tissue mass or loss of condition over the short 30-day preexperimental holding period (Chase and McMahon 1994).

Prior to determination of emersion tolerance, adult individuals of both species were randomly selected (mean shell length for *D. polymorpha* = 20.2 mm, range = 15 to 27 mm, $n = 300$; mean shell length for *D. bugensis* = 21.8 mm, range = 14 to 30 mm, $n = 296$), individually marked with an identifying number painted on the shell, wet-weighted to the nearest 0.1 mg, and reimmersed for 24 hr. After 24-hr reimmersion, separate samples of 60 mussels of both species were emersed in desiccation chambers under five different relative humidity conditions. Specific relative humidity (R.H.) levels were maintained in the desiccators over saturated salt solutions. Mussels were held above these solutions on stages constructed of 0.5-cm wire mesh covered with a 1-mm nylon mesh. Tested R.H. levels were: <5-percent R.H. maintained over silica gel desiccant; 33-percent R.H. over a saturated solution of magnesium chloride ($\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$); 53-percent R.H. over a saturated solution of magnesium nitrate ($\text{Mg}(\text{NO}_3)_2 \cdot 6\text{H}_2\text{O}$); 75-percent R.H. over a saturated solution of sodium chloride (NaCl); and >95-percent R.H. over distilled water (after Byrne, McMahon, and Dietz 1988). Desiccation chamber temperature was held at a constant $15 \pm 0.2^{\circ}\text{C}$ in a refrigerated incubator.

Periodically, subsamples of six individuals of either species were removed from each desiccator, reweighed, and their viability tested by rehydration in dechlorinated tap water for 12 hr at room temperature (22 to 24°C). After rehydration, viability was tested by touching mussels in the vicinity of the siphons and posterior mantle tissues with the tip of a small paint brush. If this stimulation did not elicit an immediate valve closure response, the individual

was considered to be dead. Subsampling frequency was designed to encompass a total duration of emersion over which subsamples exhibited 100-percent survival through to 100-percent mortality. Lethal emersion times were estimated as LT_{50} values (estimated time for 50-percent sample mortality) determined by probit analysis (Bliss 1936) and SM_{100} values recorded as the actual time to the first observation of 100-percent subsample mortality.

At the end of the recovery period, all sampled individuals were oven-dried to constant weight at 90 °C. Subtraction of specimen dry weight from initial wet weight yielded the total water weight (TW, total water weight = corporal + extracorporal water weight [i.e., body + mantle cavity water weight]). Subtraction of the wet weight after emersion from the initial, preemersion wet weight yielded the weight of water lost during the emersion period. Water loss was also expressed as the fraction of total preemersion water weight in fully hydrated individuals (after Byrne, McMahon, and Dietz 1988). Computation of mean fraction of TW lost values for subsamples of individuals removed at different periods over the course of emersion allowed estimation of cumulative water loss over tolerated emersion periods. In all cases, water loss values were only computed for individuals surviving a particular duration of emersion. In all statistical analyses, statements of significance are at an error level of $\alpha \leq 0.05$.

3 Results

Multiple Least Squares Linear Regression Analyses of the natural logarithm (ln) of the weight of water lost versus ln time of emersion, shell length, and R.H. as independent variables revealed that these independent variables explained 86 percent of all variation in weight of water lost in *D. polymorpha* and 84 percent in *D. bugensis*. Such high levels of correlation indicated little or no desiccation chamber effect on water loss rate in either species, allowing subsequent statistical analyses to utilize individual mussels as the experimental unit. For emersed specimens of *D. polymorpha* and *D. bugensis*, water loss rates were clearly correlated with R.H. Multiple Factor ANOVA indicated that the ln-transformed weight of water lost during emersion increased with the covariants of size measured as shell length (SL) and the natural logarithm of hours of emersion ($P < 0.00001$). In contrast, there was no detectable difference in the weight of water lost between the two species ($P = 0.796$). Lack of difference in water weight lost occurred in spite of a reduced pre-emersion total water weight in specimens of *D. bugensis* relative to those of *D. polymorpha* of equivalent SL (Figure 1) ($P < 0.00001$ as revealed by ANCOVA analysis of ln total water weight with SL as the covariant [$P < 0.0001$]). Best fit of a least squares linear regression of ln TW on SL of *D. bugensis* was as follows:

$$\ln \text{ TW (g)} = -3.6023 + 0.1463 (\text{SL in mm})$$

$$(n = 296, r = 0.867, F = 894, P < 0.00001)$$

This relationship for *D. polymorpha* was:

$$\ln \text{ TW (g)} = -3.2800 + 0.1379 (\text{SL in mm})$$

$$(n = 300, r = 0.869, F = 1219, P < 0.00001)$$

In contrast, water loss decreased significantly with increasing R.H. being insignificantly different between the 5-percent and 33-percent R.H. groups and the 53-percent and 75-percent R.H. groups, but significantly different between these two groups and mussels exposed to 95-percent R.H. (Table 1). Similar results were recorded for water loss expressed as a percent of TW (PTW) excepting a lack of correlation between SL and PTW lost (Table 2). These results indicate that while smaller individuals lost smaller actual volumes of

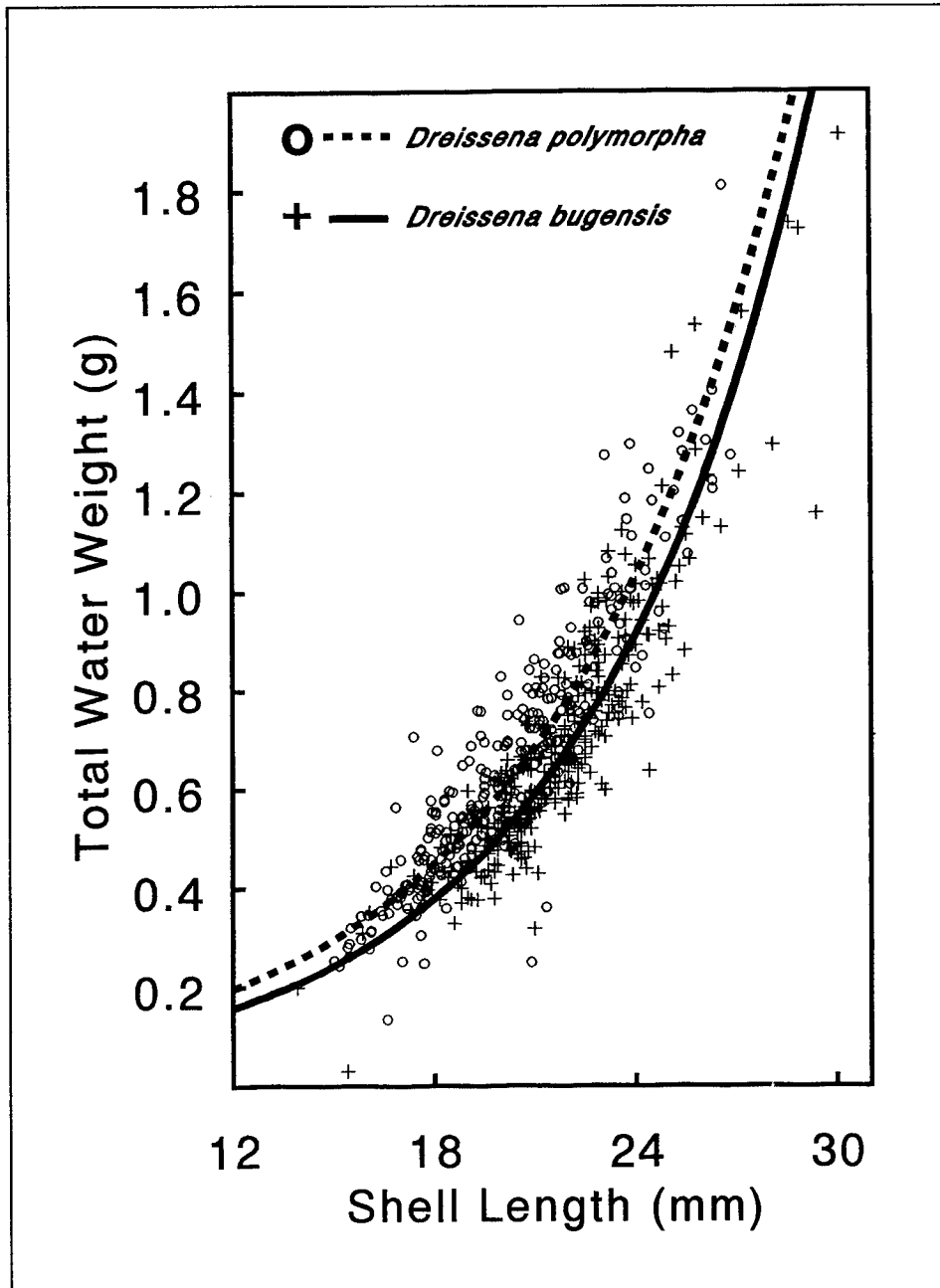


Figure 1. The relationship between total water weight (TW = corporal + extra-corporal mantle cavity water weight in grams) (vertical axis) and shell length (SL in mm) (horizontal axis) of adult specimens of *Dreissena bugensis* (crosses) and *Dreissena polymorpha* (open circles)

water than did larger individuals, relative water loss expressed as a percentage of total available water was independent of size over the experimental SL range of 14 to 30 mm.

Multiple Factor ANOVA testing indicated that the mean PTW lost just prior to death (i.e., mean percent of TW lost of individuals in the sample just

Table 1
Multiple Factor ANOVA for Testing for Differences in Mean in Cumulative Total Water Weight Lost in Specimens of *Dreissena polymorpha* (zebra mussel) and *Dreissena bugensis* (quagga mussel) Emerged at 15 °C Under Different Relative Humidities

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square Error	F-Ratio	Probability
Covariate Shell Length	28.98	1	28.98	28.77	<0.00001 ¹
Covariate in Hours Emerged	123.95	1	123.95	123.06	<0.00001 ¹
Species	0.089	1	0.089	0.089	0.769
Relative Humidity	190.06	4	47.51	47.17	<0.00001 ¹
Residual	279.00	277	1.01		
Total	516.52	284			

¹ Significant effect at $P \leq 0.05$.

Student Newman-Keuls Tests of Differences in Mean in Cumulative Total Water Weight Lost Between Different Relative Humidity Treatments for Specimens of *Dreissena polymorpha* and *Dreissena bugensis* Emerged at 15 °C

Percent Relative Humidity	Mean	n	Signif. Diff. ($P \leq 0.05$)
<5	-1.102	46	--
33	-1.448	48	--
53	-2.002	62	--
75	-2.308	69	--
>95	-3.855	60	--

preceding the sample in which greater than 60-percent mortality was recorded) was significantly different under different R.H. treatments ($P < 0.0001$) and between the two species ($P < 0.0151$), but was not correlated with SL ($P > 0.649$) (Table 3). Percent of TW lost just prior to death was least at >95-percent R.H., and insignificantly different between 53- and 75-percent R.H. treated mussels and <5- and 33-percent R.H. treated mussels. The percent of TW lost just prior to death values recorded in these 53- and 75-percent R.H. and <5- and 33-percent R.H. groups were significantly different from each other, and both were different from that recorded at >95-percent R.H. (Table 3).

Table 2
Multiple Factor ANOVA for Testing for Differences in Mean in Cumulative Total Water Weight Lost in Specimens of *Dreissena polymorpha* (zebra mussel) and *Dreissena bugensis* (quagga mussel) Emerged at 15 °C Under Different Relative Humidities

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square Error	F-Ratio	Probability
Covariate Shell Length	0.0038	1	0.0038	0.004	0.951
Covariate in Hours Emerged	125.04	1	125.04	127.31	<0.00001 ¹
Species	0.462	1	0.462	0.47	0.501
Relative Humidity	195.39	4	48.85	49.73	0.00001 ¹
Residual	272.08	277	0.98		
Total	493.80	284			

¹ Significant effect at $P \leq 0.05$.

Student Newman-Keuls Tests of Differences in Mean in Cumulative Percent Total Water Weight Lost Between Different Relative Humidity Treatments for Specimens of *Dreissena polymorpha* and *Dreissena bugensis* Emerged at 15 °C

Percent Relative Humidity	Mean	n	Signif. Diff. ($P \leq 0.05$)
<5	3.858	46	--
33	3.491	48	--
53	2.979	62	--
75	2.653	48	--
>95	1.064	46	--

When mean PTW lost just prior to death values were compared across species, values were similar for *D. polymorpha* and *D. bugensis* at relative humidities of <5 percent through 53 percent at approximately 45 to 60 percent of total water. In *D. bugensis*, PTW lost just prior to death declined to <30 percent at 75-percent R.H. and <10 percent at <5-percent R.H. (Figure 2). In contrast, PTW lost just prior to death at 33-percent R.H. in *D. polymorpha* remained similar to that recorded at lower R.H. and declined to <30 percent of total water only in the >95-percent R.H. treatment. Thus, at 75- and >95-percent R.H., PTW lost just prior to death was 2 to 3 times greater in *D. polymorpha* than in *D. bugensis* (Figure 2).

Table 3
Multiple Factor ANOVA for Testing for Differences in Mean in Cumulative Percent of Total Water Just Prior to Death Under Different Relative Humidities in Specimens of *Dreissena polymorpha* (zebra mussel) and *Dreissena bugensis* (quagga mussel) Emerged at 15 °C

Source of Variation	Sum of Squares	Degrees of Freedom	Mean Square Error	F-Ratio	Probability
Covariate Shell Length	41.38	1	41.377	0.217	0.649
Species	1,223.99	1	1,223.99	6.418	0.0151 ¹
Relative Humidity	12,030.94	4	682.19	3,007.73	<0.00001 ¹
Interaction	2,728.76	4	682.19	3.577	0.0134 ¹
Residual	8,009.74	42	190.71		
Total	24,564.03	52			

¹ Significant effect at $P \leq 0.05$.

Student Newman-Keuls Tests of differences in Cumulative Percent Total Water Lost Just Prior to Death Under Different Relative Humidities for Specimens of *Dreissena polymorpha* and *Dreissena bugensis* Emerged at 15 °C

Percent Relative Humidity	Mean	n	Signif. Diff. ($P \leq 0.05$)
33	54.76	9	--
<5	53.42	11	--
53	50.29	11	--
75	38.36	10	--
>95	15.54	12	--

The reduced PTW lost just prior to death in specimens of *D. bugensis* <75- and >95-percent R.H. was also reflected in the cumulative water loss rates of emerged specimens of this species. At <5-, 33-, and 53-percent R.H., cumulative PTW lost was essentially similar between the two species over their tolerated emersion periods (Figures 3A-C); however, at 75- and 95-percent R.H., cumulative PTW lost did not increase as rapidly in *D. bugensis* with duration of emersion as it did in specimens of *D. polymorpha* leading to the reduced PTW lost just prior to death values recorded for *D. bugensis* at these two elevated R.H. treatments (Figures 3D and E).

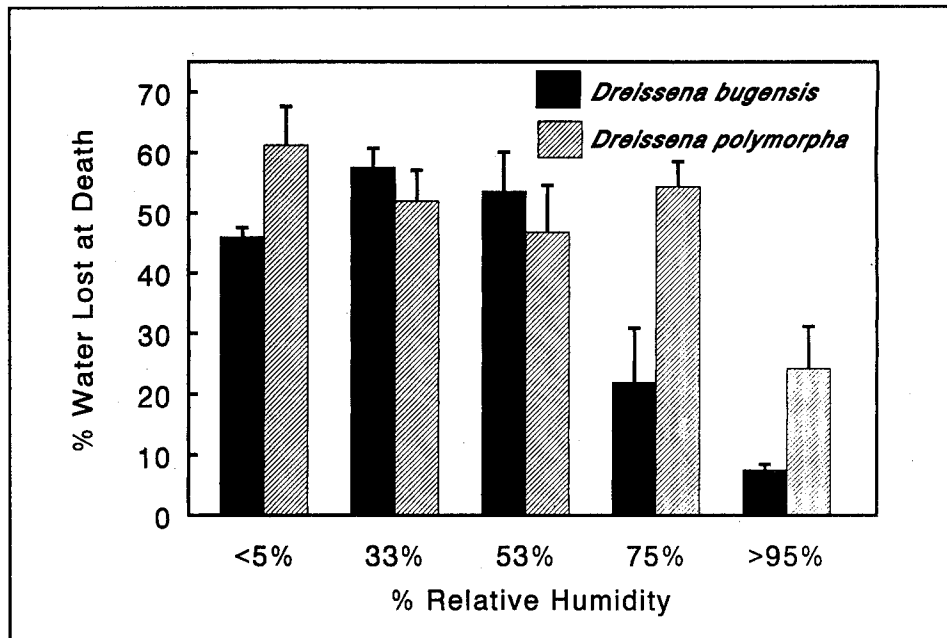


Figure 2. Mean percent (+ standard error) of total water (corporal + extra-corporal mantle cavity water) lost just prior to death (vertical axis) by specimens of *Dreissena bugensis* (solid histograms) and *Dreissena polymorpha* (cross hatched histograms) at various relative humidities (horizontal axis)

Measured as LT_{50} values (estimated time for 50-percent sample mortality, Bliss 1936), desiccation tolerance was essentially similar in specimens of *D. polymorpha* and *D. bugensis* across all R.H. treatments (Figure 4A) in spite of lower PTW lost just prior to death values recorded for *D. bugensis* (Figure 2). In contrast, times to actual 100-percent sample mortality (SM_{100}) were 25 percent to nearly 100 percent greater in *D. polymorpha* at the higher R.H. treatments of 53, 75, and >95 percent (Figure 4B).

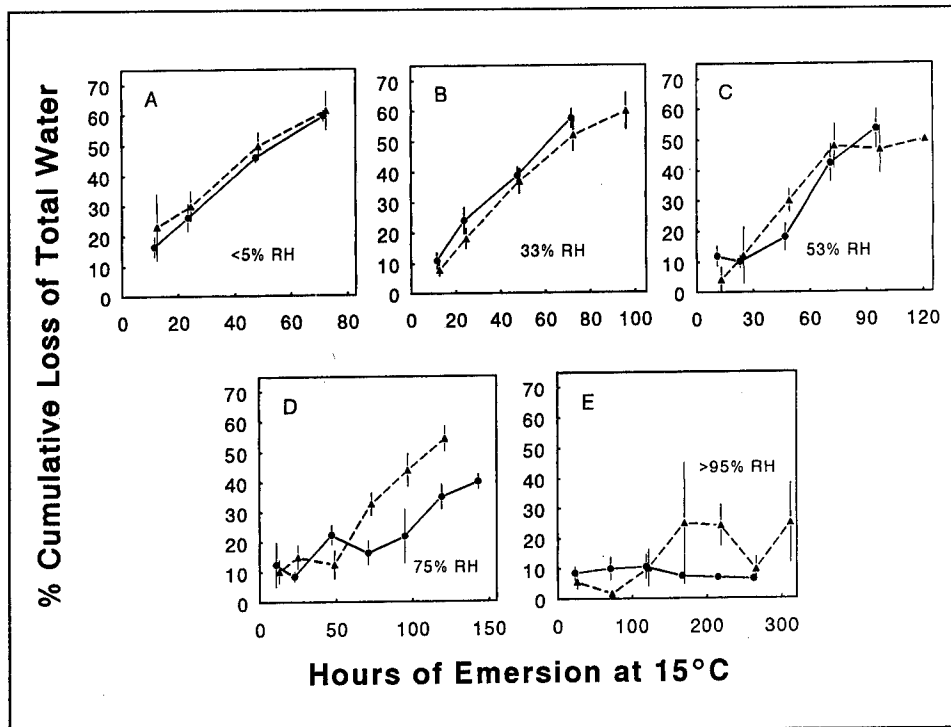


Figure 3. Mean cumulative percent (+ standard error) of total water (corporal + extracorporal mantle cavity water) lost during emersion (vertical axis) by specimens of *Dreissena bugensis* (solid triangles and dashed lines) and *Dreissena polymorpha* (solid circles and solid lines) during emersion at 15 °C in relative humidities of (A) <5 percent, (B) 33 percent, (C) 53 percent, (D) 75 percent, and (E) >95 percent

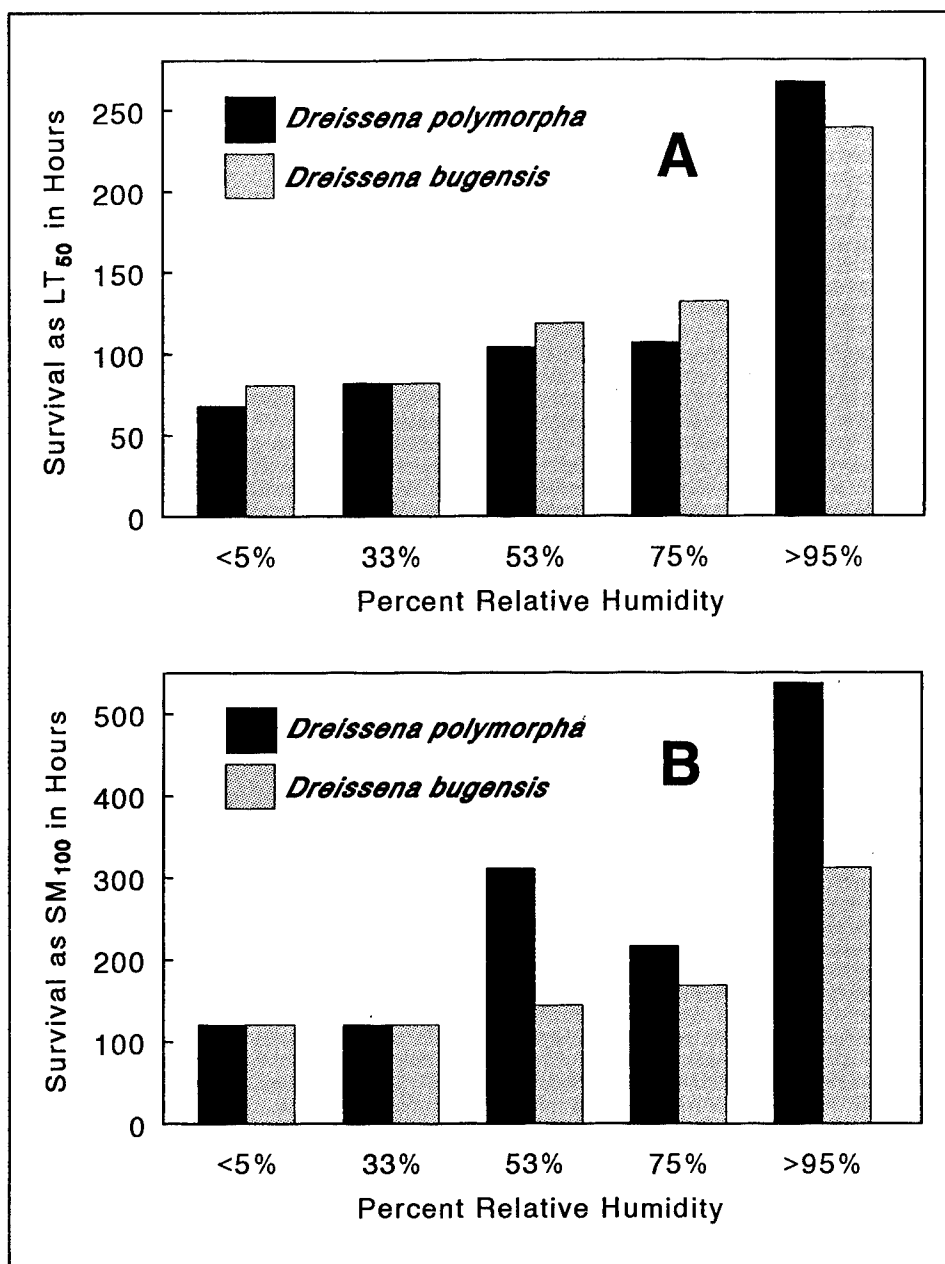


Figure 4. Emersion tolerance in *Dreissena bugensis* and *Dreissena polymorpha* at 15 °C and various relative humidities (horizontal axis)

4 Discussion

Until very recently, dewatering and exposure to lethal desiccation have had no experimental attention as a potential dreissenid macrofouling mitigation strategy. The only previously available information on desiccation tolerance in zebra mussels came indirectly from a study of their capacity to buffer the hemolymph (i.e., blood) pH while emersed. Mussels emersed at room temperature (20 to 22 °C) without controlled R.H. in this prior study survived emersion no longer than four days (Alyakrinskaya 1978).

McMahon, Ussery, and Clarke (1993) described experiments designed to determine the effects of R.H. and temperature on emersion tolerance in *D. polymorpha*. Multiple Linear Regression models were developed which could be utilized to estimate LT_{50} and SM_{100} times based on emersion temperature and R.H. conditions. Results showed that emersion tolerance increased exponentially with declining temperature and increased linearly with increased R.H. At 25 °C, R.H. had little effect on lethal emersion times in *D. polymorpha* with 4 to 5 days required for 100-percent mortality, a level of emersion tolerance similar to that reported by Alyakrinskaya (1978). However, at temperatures below 25 °C, relative humidity became an increasingly important factor such that emersion durations at temperatures below 15 °C, particularly at higher R.H., were extended beyond 10 days, rendering the recommended practice of holding of recreational boats out of water for 2 to 5 days to kill attached zebra mussels prior to transportation between water bodies (Ontario Ministry of Natural Resources 1990, 1991a, 1991b) unlikely to be effective except during the warmest summer months. For similar reasons, it was suggested that dewatering of mussel-infested structures for mitigation of zebra mussel fouling was likely to be most efficacious at ambient air temperatures above 20 °C where emersion tolerance times were relatively short (<5 days) regardless of R.H. (McMahon, Ussery, and Clarke 1993).

Our present results indicate that, at 15 °C, the emersion tolerance of *D. bugensis* expressed as LT_{50} or SM_{100} values was either equivalent to or less than that of *D. polymorpha* over a relative humidity range of <5 to >95 percent. The equivalency of emersion tolerance between *D. bugensis* and *D. polymorpha* strongly suggests that the emersion times reported to be effective in mitigating infestations of *D. polymorpha* (McMahon, Ussery, and Clarke 1993) will also be efficacious in mitigating *D. bugensis* macrofouling.

Our data suggest that both quagga and zebra mussels are relatively intolerant of prolonged emersion relative to other freshwater bivalve species. At 15 °C between <5- and 75-percent R.H., Asian clams (*Corbicula fluminea*) can tolerate emersion more than twice as long as *D. polymorpha* or *D. bugensis* (Dreissenid SM₁₀₀ range = 115-530 hr, Figure 4B) (Byrne, McMahon, and Dietz 1988). Both freshwater unionid and sphaeriid bivalves appear to be much more tolerant of emersion than *D. polymorpha* or *D. bugensis*. Riverine and pond unionids and sphaeriids can survive many months' emersion at high temperatures when exposed to air by receding water levels during droughts and dry seasons (for a review see McMahon 1991), while zebra and quagga mussels can survive a maximum of only 22 days in water-saturated air (>95-percent R.H.) at a relatively low temperature of 15 °C (Figure 4B).

The very reduced emersion tolerance of dreissenids relative to unionid and sphaeriid bivalves suggests that they, like the emersion-intolerant *C. fluminea*, are only recent invaders of freshwaters (McMahon 1991). The frequency and duration of emersion experienced by intertidal bivalves is much shorter and more predictable than that experienced by freshwater bivalves; thus, marine species are generally less tolerant of emersion than freshwater bivalves (McMahon 1991). Neither zebra mussels nor Asian clams appear to have had a long-enough evolutionary history in fresh water to have fully evolved the high levels of emersion tolerance characteristic of most freshwater unionid and sphaeriid bivalve species, whose evolutionary histories in fresh water extend from the Triassic and Cretaceous periods, respectively (McMahon 1991).

At 15 °C, PTW loss prior to death in zebra mussels ranged from 45 to 60 percent over <5- to 53-percent R.H. in both *D. polymorpha* and *D. bugensis*. This range of tolerated water loss was similar to that of specimens of *C. fluminea* emersed under similar conditions (~50 to 80 percent) (Byrne, McMahon, and Dietz 1988) and falls within that reported for three species of freshwater unionids more tolerant of emersion than zebra mussels (Holland 1991). The similarity of PTW loss prior to death values for zebra mussels emersed in <5- to 53-percent R.H. to that reported for other freshwater bivalve species suggests that mussels emersed under these conditions died as a result of lethal tissue desiccation. At 75-percent R.H., the PTW lost prior just to death in *D. polymorpha* remained above 50 percent, suggesting that death also resulted from lethal tissue desiccation at this relatively high R.H. In contrast, PTW loss just prior to death was only 22 percent at 75-percent R.H. in *D. bugensis* (Figure 2). At >95-percent R.H., PTW lost just prior to death in both *D. polymorpha* (23 percent of TW) and *D. bugensis* (8 percent of TW) was considerably below that recorded at relative humidities of 53 percent or less (Figure 2). The occurrence of mortality at elevated R.H. at lower than maximally tolerated levels of desiccation suggests that death of emersed specimens of *D. polymorpha* at >95-percent R.H. and *D. bugensis* at 75- and >95-percent R.H. was not due to lethal tissue desiccation. Rather, some other emersion-induced stress such as accumulation of toxic anaerobic metabolites, disruption of hemolymph acid-base balance, ammonia toxicity, or exhaustion of organic energy stores must have been the cause of death (for reviews see McMahon 1991, Byrne and McMahon 1994).

When emersed at high relative humidities, shallow-water, emersion-tolerant freshwater bivalves including unionids (Holland 1991; Byrne and McMahon 1994) and *C. fluminea* (Byrne, McMahon, and Dietz 1990) and marine intertidal bivalves (McMahon 1988) periodically gape the valves, allowing uptake of oxygen across the exposed epithelial surfaces of mucus-fused mantle edges. Such periodic aerial gas exchange behavior allows maintenance of an aerobic catabolism but results in elevated water loss rates. In contrast, deeper water bivalves, not adapted to periodic emersion, keep the valves tightly closed in air and catabolize anaerobically. While this behavior greatly reduces water loss, it results in the rapid accumulation of toxic anaerobic metabolic end-products to lethal levels. Thus, even though emersed deep-water bivalve species often lose water at a slower rate than do shallow water species, they are generally less tolerant of aerial exposure because of their dependence on anaerobic rather than aerobic catabolism. (McMahon 1988; Byrne and McMahon 1994 and references therein).

While emersed at high relative humidities, specimens of *D. polymorpha* were observed to periodically gape the valves and expose mantle tissues, allowing aerial gas exchange. In contrast, specimens of *D. bugensis* gaped only when approaching death. Suppression of mantle edge exposure behavior in *D. bugensis* in high relative humidities may have led to the reduced water loss rates recorded at 75- and >95-percent R.H. relative to that of *D. polymorpha* (Figures 3D and E) and could have accounted for the very reduced PTW lost just prior to death at 75- and >95-percent R.H. (22 and 8 percent of total water, respectively, Figure 2), particularly if maintenance of shut valves caused rapid accumulation of toxic anaerobic end-products to lethal levels.

In Lake Erie, the proportion of individuals of *D. bugensis* in mixed zebra/quagga mussel populations changes with increasing depth, averaging 1-50 percent of mussels in shallow, near-shore waters and increasing to 100 percent of the population at depths below 20 m, with living specimens found at depths of up to 63 m (Dermott 1993). In contrast, *D. polymorpha* populations generally reach maximum densities between depths of 1 and 16 m and do not extend below the thermocline (Mackie et al. 1989). Thus, *D. polymorpha* populations can be periodically emersed by natural changes in water level, while the more deeply distributed *D. bugensis* would rarely experience emersion. This difference in depth distribution helps explain the zebra mussel's greater emersion tolerance, reflected in elevated SM_{100} values, at high R.H. (Figure 4B). In addition, specimens of *D. polymorpha* emersed at high R.H. display periodic mantle edge exposure behavior for aerial gas exchange and correspondingly elevated water loss rates characteristic of shallow-water, emersion-tolerant freshwater bivalve species. In contrast, specimens of *D. bugensis* emersed in high R.H. maintain closed valves likely to result in anaerobic catabolism, leading to rapid accumulation of anaerobic end-products to lethal levels typical of emersion-intolerant deep-water bivalve species.

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R.H. and in *D. bugensis* at 75- and >95-percent R.H., suggesting that, at higher R.H., death did not result from desiccation, but from accumulation of toxic anaerobic end-products. Emersion tolerance measured as SM_{100} values was reduced in *D. bugensis* compared with *D. polymorpha* at 53- to >95-percent R.H. The reduced SM_{100} values of *D. bugensis* and very low fraction of TW lost by this species just prior to death at 75- and >95-percent R.H. relative to *D. polymorpha* reflect its general restriction to greater depths where probability of emersion is low. Overall, emersion tolerance in both species is reduced compared to native North American bivalves. Recommended emersion times for mitigation of *D. polymorpha* fouling will also be effective for *D. bugensis*.